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Home-ranges of tropical Red-capped Larks are influenced by breeding rather than vegetation, rainfall or invertebrate availability

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Home-range studies have received considerable attention from ecologists but are greatly skewed towards the north temperate areas. Tropical areas offer an ideal setting to tease apart hypotheses about weather, food availability and social interactions as important factors influencing home-range. In this study, we investigated home-range and movement patterns of the tropical Red-capped Lark *Callandrella cineria*, a year-round breeding bird with a dynamic social structure. We tracked 56 individuals using radiotransmitters and colour-ring readings over a 23-month period. Our objective was to understand year-round variation in home-range size in the context of the highly aseasonal and unpredictable variation in weather and resources typical of many equatorial habitats, in addition to the birds' changing social structure and year-round breeding. The mean composite monthly home-range of Red-capped Larks was 58.0 ha, and the mean individual home-range size was 19.9 ha, but this varied considerably between individuals. The total number of nests found per month (breeding intensity) best predicted home-range size of non-breeding birds, and of breeding and non-breeding birds combined. We show for the first time that breeding intensity decreases the home-range size of non-breeding individuals. Our study also underlines the relevance of conducting more studies in aseasonal tropical areas in order to disentangle effects of weather, food availability and breeding that vary in parallel, peaking simultaneously in most seasonal areas.

Keywords: aseasonal, composite, transmitters, year-round breeding.

In many animals, survival and reproduction depend on the general habitat type and the specific resources available within an individual's home-range (Odum & Kuenzler 1955, Germain *et al.* 2015). Understanding the factors influencing home-range size therefore provides insights into a species' ecology (Ofstad *et al.* 2016). The availability of structural and functional resources such as nest-sites and food availability can change with time, for

example over months, seasons or years (Wiebe & Gow 2013). The home-range is therefore not static but likewise varies over time (Takano & Haig 2004). In addition to varying with time, habitats are spatially heterogeneous, and within an individual's home-range, different areas may be suitable for different life-cycle events (Orians & Wittenberger 1991). Movement decisions within the home-range and intensity of utilization of the different areas are therefore important factors in influencing performance (Fuller & Harrison 2010).

Home-range size and intensity of utilization of the different areas within a home-range depend on environmental factors such as weather conditions and food resources (Rolando 1998), but also on life cycle and social factors such as breeding (Börger *et al.* 2006, Saïd *et al.* 2009, Holland *et al.*

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2017). Weather patterns determine the need for shelter and the accessibility of food resources (Tieleman & Williams 2000). In most organisms, home-range size is inversely related to the abundance of food (Margalida *et al.* 2016). In many habitats, food availability, abundance and distribution change under the influence of weather and season. In response to such change, organisms may remain within the same home-ranges, increase or decrease home-range size, or completely move to different home-ranges. How individuals respond to habitat heterogeneity within the home-range and/or spatial and temporal resource change will also depend on their reproductive status (Anich *et al.* 2010), sex (Holland *et al.* 2017) and social organization (Margalida *et al.* 2016). Birds have been shown to increase home-range size from non-breeding to breeding periods due to putative higher nutritional demands of the breeding season, while at the same time during breeding periods, movement is often limited and central to the location of nests (van Beest *et al.* 2011). Birds also change social organization through fission–fusion dynamics where large groups break into smaller groups or vice versa to adjust their socio-spatial structure to changing environmental conditions and resource availability (Griesser *et al.* 2009, Silk *et al.* 2014). To prepare for breeding, birds can also change their social organization from flocks to pairs, or engage in territorial defence that excludes non-breeding individuals from accessing some areas. However, in a system with year-round breeding, how the number of breeding birds in a population affects the home-ranges of breeding and non-breeding individuals where both statuses frequently co-occur is currently unknown.

Studies investigating home-range in birds have primarily been conducted on temperate zone birds, with only a few exceptions focusing on tropical birds, especially Afro-tropical residents (Baldwin *et al.* 2010). The strong ‘temperate zone bias’ may lead to biased interpretations of the causes and correlates of home-range variation, as birds in the tropics and temperate regions experience very different conditions. In addition, interpretation of variation in home-range size is hampered by the fact that animals breed when resources are plentiful in temperate zones, and thus it is difficult to tease the different effects apart. Even fewer studies have quantified home-range sizes of resident non-migratory species at small temporal scales (e.g. monthly) and over longer time periods such as years

(Tsao *et al.* 2009). With the majority of home-range and movement studies focusing on temperate zone environments, where annual and seasonal changes of weather and associated resources are predictable, unpredictable low-latitude environments remain understudied. Yet, unpredictable weather patterns and resource availability observed in the tropics coupled with a diversity of life history strategies, even within a population, make the tropics ideal for the study of the drivers of animal-movement patterns. In addition, studying home-range variation at smaller scales can be relevant for conservation, especially in heterogeneous landscapes where habitat specialists might be confined to very specific habitats (Bevanda *et al.* 2015).

Red-capped Larks *Callandrella cineria* are small, gregarious birds found in short-grass and bare-ground habitats widely distributed across Africa (Zimmerman *et al.* 2005). They feed on a variety of insects and seeds (Ndithia *et al.* 2017a, Mwangi *et al.* 2018). Tropical populations of Red-capped Larks, with year-round breeding at the population level and frequent co-occurrence of breeding and non-breeding individuals (Ndithia *et al.* 2017a,b), provide an ideal study system to tease apart effects of breeding intensity, weather and food availability on home-range. Breeding year-round conveys the advantage of comparing the home-range of birds under an energetically expensive life history stage of breeding with non-breeding birds experiencing the same environmental conditions. Likewise, the abundance of invertebrates, the main food for Red-capped Larks, is unpredictable and not linked to weather patterns (Ndithia *et al.* 2017b, Mwangi *et al.* 2018, J. Mwangi *et al.* unpublished data), and neither weather patterns nor food availability explains timing of breeding (Ndithia *et al.* 2017a). The Red-capped Lark’s shift in social structure, congregating in mixed-sex flocks when not breeding (fusion) and splitting up into pairs during breeding (fission; Ndithia *et al.* 2017a, Mwangi *et al.* 2018), suggests that changes in habitat use are an essential component of its life history. Studying their home-range and movement patterns over multiple years can provide insights into their habitat needs during different life cycle stages, independent of the time of the year.

In this study we investigated home-range sizes of resident equatorial Red-capped Larks during a 23-month period (August 2014–June 2016). We explored how month-to-month variations in home-range sizes were associated with variation in

weather, food availability and breeding intensity, based on the entire dataset, and based on non-breeding birds only. We also compared, at the individual level, the home-range sizes of non-breeding and breeding individuals. At the population level, we predicted that home-range size: (1) would be negatively correlated with monthly rainfall due to its favourable effect on food availability, and likewise negatively correlated with enhanced vegetation index (EVI) and invertebrate abundance as proxies for food availability, and (2) would decrease at the population level when more birds were breeding and hence confined to the nest. When restricting these analyses to the non-breeders only, we expected no association between home-range and breeding intensity. Finally, we predicted sex differences in home-range due to different roles, especially during breeding, when males are predicted to be more active in defending their nesting areas than females (J. Mwangi pers. obs.).

METHODS

Study area and study species

We studied Red-capped Larks in Kedong Ranch, Naivasha, Kenya (00°53.04'S, 036°24.51'E, 1890 m above sea level). Our study area, Kedong Ranch, is a privately owned ranch with extensively grazed grasslands, sandwiched between Mt Longonot and Hell's Gate National Parks on the floor of the Rift Valley escarpment.

Bird capture and tracking

During the period March 2014–June 2016, we captured 620 Red-capped Larks using mist-nets and ringed each bird with a numbered aluminium metal ring, in addition to a unique combination of three UV-resistant colour bands (Appendix S1). We monitored movement patterns throughout the study area to record bird locations 6 days a week. Between May 2015 and March 2016, we also tagged 50 birds with VHF radiotransmitters, each transmitting at a unique frequency and with a battery life of 6 months (JDJC Corp., Dewey, IL, USA) to allow more detailed tracking. Transmitters weighed 0.9 g, which was on average $3.7\% \pm 0.3$ sd (range 2.5–4.4%, $n = 46$) of the bird's mass (mean $24.0 \text{ g} \pm 1.7$ sd, $n = 695$). We fitted the transmitters using a backpack loop (Pimentel & Hansbauer 2013). We tracked

radiomarked birds by homing on foot using hand-held radio receivers (SIKA Radio Tracking Receiver, Biotrack Ltd, Wareham, UK) attached to a three-element flexible antenna (Yagi 173 MHz, Biotrack). We approached slowly when the signal indicated that the bird was close (≤ 30 m). When the signal was above 95% (≤ 15 m) we detected the bird visually with binoculars and telescope, and recorded the location with a GPS (Garmin, Kansas City, KS, USA). We searched for birds 6 days a week for 8 h/day, targeting a minimum of one fix per bird per week. For birds for which we did not receive a signal, we searched the immediate areas (10×10 km grid) around the study site once a week using a car-mounted receiver (Appendix S1).

Molecular sexing

To determine the sex of our birds, we collected a small blood sample upon capture from the brachial wing vein in the field. The blood samples were then carried on ice and stored in a freezer until laboratory analysis (see Ndithia *et al.* 2017b). We extracted DNA from red blood cells using an ammonium acetate method (Richardson *et al.* 2001) and determined sex following Van der Velde *et al.* (2017).

Weather, EVI, invertebrates and breeding intensity

We recorded rainfall and temperature using weather stations (2011–2014, Alecto WS-3500, Den Bosch, the Netherlands; 2014–2016, Vantage Vue, Davis, the Netherlands) located within the study site. To measure vegetation change, we used the EVI, which has been shown to be more accurate than the normalized difference vegetation index (NDVI), as the latter does not correct for variations in solar angle (Matsushita *et al.* 2007). We downloaded MODIS EVI 16-day composite grid data (MOD13Q1 tile h21v09) for the entire study site in HDF format from August 2014 to June 2016 (45 composite periods) from the USGS Earth explorer. For each composite period, we extracted the EVI and reprojected the images in the WGS84 projection. We then cleaned the raw EVI data stack using the quality data stack to generate a clean EVI raster layer (Hijmans 2016). We extracted time series EVI data by clipping the study area and taking the EVI of evenly spaced coordinate points separated by double the ground

pixel size of the EVI MODIS satellite to avoid taking values from the same quadrant. We calculated the mean monthly EVI value for each month by averaging all EVI time series values falling within the month.

We measured ground invertebrate biomass using pitfalls, and flying invertebrate biomass using sweep nets once a month (Ndithia *et al.* 2017a, Mwangi *et al.* 2018). We recorded ground and flying invertebrates in all months with the exception of December and October 2015, due to tampering of the pitfall traps by local herders. Briefly, we used four transects subjectively selected as representative of vegetation within the study area with five plastic cups each, inserted in the ground and half filled with formaldehyde to preserve invertebrates, which we then harvested after 5 days in the field. We also walked along the transects with a sweep net on the day we collected the contents of pitfalls. We then identified all contents, sorted them to taxonomic groups based on morphology, and used a category-specific calibration curve relating dry mass as a function of length and width to estimate biomass (Ndithia *et al.* 2017a).

We searched for nests, on average (\pm se), for 20 ± 1.0 days per month (range 7–31 days/month) and 245 ± 31.2 h/month (range 17–825 h/month) during the study period (Mwangi *et al.* 2018). To quantify breeding intensity, we calculated a monthly nest index, defined as the total number of nests found in a month per 10-person hours of search effort. We did this because our search effort varied over time, but the area searched for nests was constant during the entire study period (Ndithia *et al.* 2017a,b, Mwangi *et al.* 2018).

Statistical analysis

Nature of the data and approaches used in data analysis

Our dataset is robust as a result of continuous daily tracking of birds over a 23-month period. Following the assumption of a stochastic environment (Ndithia *et al.* 2017a,b, Mwangi *et al.* 2018), we measured all factors at a finer temporal resolution of the month compared with the coarser temporal scale of season used in most seasonal studies. In addition, individuals were tracked for long time periods (varying from 4 to 21 months), covering multiple breeding and non-breeding phases as well as repeated changes in social organization from group living to pair

formation. However, the number of location fixes varied among individuals and among months, often with few fixes per individual per month (Appendix S1). Although breeding birds were well represented, our dataset was biased towards non-breeding birds (Appendix S2). This partly resulted from having to define the breeding period as the period during which an individual was attending its nest (nest-building until fledging), a period lasting 24 days in this species (Mwangi *et al.* 2018). Following our sampling protocol as described earlier, we obtained too few positions per individual per week/month to warrant an analysis of home-range size in relation to breeding stage at the individual level.

To explore home-range sizes and their associations with weather, food availability and breeding, we combined two approaches and used two methods for estimation of home-range size: the minimum convex polygon (MCP; White & Garrott 1990) and kernel density estimation (KDE; Worton 1985). MCP creates a geometrically bound polygon containing all locations of birds, i.e. 'fixes', where all vertices are convex, whereas KDE estimates the probability that an individual uses an area defined by a series of density isopleths (Worton 1985, White & Garrott 1990).

To describe home-range variation among individuals within the population and to compare males with females, we calculated home-ranges for each individual based on all its location fixes collected over the entire 23-month period using KDE with least squares cross-validation (Worton 1995). To determine how weather, food availability and breeding intensity were associated with home-range sizes, we computed a composite home-range for the population per month based on all observations from all individuals within a given month using MCP, because within a single month we had too few location fixes per individual to compute monthly home-ranges at the individual level (White & Garrott 1990, Seaman *et al.* 1999). Although we are aware of the debate on the limitations of MCP (Nilsen *et al.* 2008), we used the method to calculate composite home-ranges because we were interested in the geometrically bound area containing all locations of birds within that month (Minderman *et al.* 2010).

Spatial and temporal patterns of habitat use

To show how the spatial distribution of birds changed through time, we plotted per month all

locations where each marked individual was sighted on the study site (using the R package *ggplot2*; Wickham 2009). We assumed that the probability of sighting a bird was the same for marked and unmarked birds and therefore that our marked bird observations reflected movement patterns of the entire population. To calculate composite home-ranges for the population for each month, we merged the median centres and median axes of individual birds (Fig. 1). We calculated these home-ranges based on 95% MCP including all birds for which we had at least two fixes per month. Because home-range estimates of individual birds are sometimes affected by the number of fixes (Seaman *et al.* 1999), we explored the influence of number of fixes per bird in a month on the home-range estimate for that month. To do so, we used data from July–October 2015, during which we observed individuals with 12 fixes per month. From this dataset, we randomly selected 2–12 fixes per individual, each time calculating the resulting monthly home-range. We repeated this five times and concluded that in our dataset, the number of fixes per individual did not affect home-range size estimates ($P > 0.05$).

Home-range size of individual birds and effect of sex on individual home-range

We calculated individual home-range for 56 Red-capped Larks (31 males, 21 females, 4 not sexed) with more than 30 fixes (Seaman *et al.* 1999). These constituted birds whose location fixes were based on reading colour rings ($n = 26$), combined colour ring reading and transmitter tracking ($n = 26$) or transmitter tracking only ($n = 4$; see Appendix S1 for details per bird). In this study, we used the term home-range as defined by Burt (1943) to mean the area normally traversed by an individual animal or group of animals during activities associated with feeding, resting, reproduction and shelter-seeking. In addition to quantifying individual home-range size, we also calculated core areas at 50% kernel (Calenge 2006). We checked whether the number of fixes per bird influenced individual home-range measures using linear models. We similarly checked whether the method used to obtain location fixes (i.e. ring reading, transmitters or a combination) influenced our individual home-range measures by comparing their individual home-ranges using an ANOVA test.

We compared individual home-ranges of males and females based on 95% kernel individual home-ranges (log-transformed) and 50% kernel core areas (log-transformed) using independent *t*-tests. We performed all statistical analyses in R 3.3.0 (R Core Team 2016).

Effects of weather, food availability and breeding on composite home-range

We investigated how weather (rainfall, T_{\min} , T_{\max}), food availability (EVI and ground and flying invertebrate biomass) and breeding intensity were associated with Red-capped Lark composite home-ranges. Prior to model selection, we checked for collinearity among explanatory variables with a variance inflation factor (VIF). Collinearity was low (the highest VIF was 2.9) and thus all explanatory variables were considered in the modelling approach (Zuur *et al.* 2010). To allow an accurate assessment of their relative effect sizes based on model-averaged parameter estimates, we standardized each variable by subtracting its mean from each value and dividing the resulting vector by the standard deviation of the variable before running the models (Galipaud *et al.* 2017). We square root-transformed monthly composite home-range for normality and applied a general linear model with rain, maximum and minimum temperature, EVI, ground and flying invertebrate biomass and breeding intensity. We used Akaike's information criterion with small sample bias adjustment (AICc) to identify the most parsimonious model. We ranked all models in order of their AICc (Burnham & Anderson 2002, Grueber *et al.* 2011). We calculated a weighted average of the parameter estimates and 95% confidence limits for all the variables contained in the models that had a summed weight ≤ 0.95 with the package MuMIn (Grueber *et al.* 2011, Barton 2018). We considered factors as significant in the model average results if the upper and lower limits of the 95% confidence intervals did not include zero.

To compare differences in composite home-range between breeding and non-breeding birds, we first computed and plotted their respective composite home-ranges for the entire study period. We then tested whether weather, food availability and breeding influenced monthly composite home-ranges of both breeding and non-breeding birds by first running the models on composite home-ranges derived from all the birds, and then re-running the

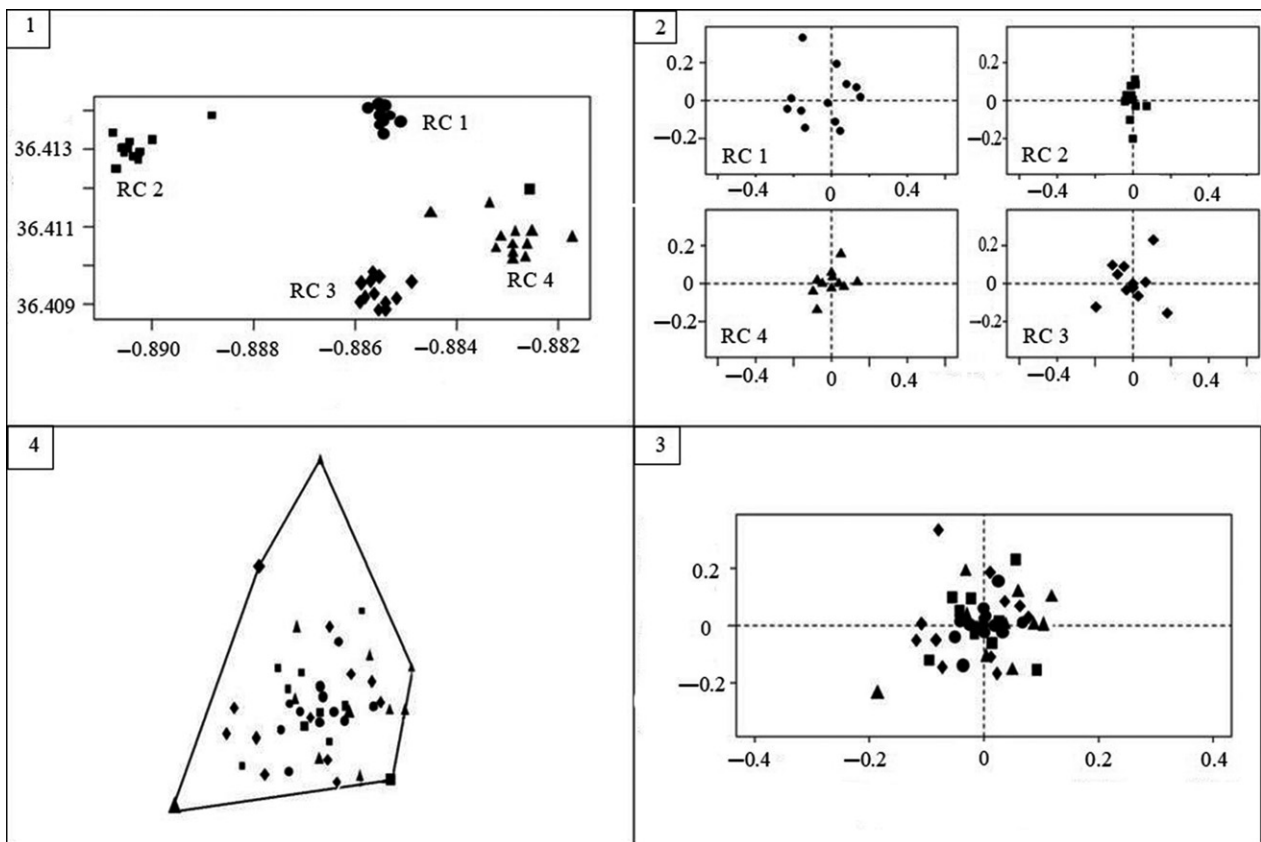


Figure 1. Stepwise illustration of how to combine and assemble fixes of individual birds within a month to create a common median centre and axes for calculation of a composite home-range for the population for that month, showing an example of four individual Red-capped Larks (RC1–4). Step 1: Plot monthly fixes of sighted birds. Step 2: Calculate the median point of the monthly fixes (separately for each individual) and re-plot the fixes around its median with a local x, y coordinate (the median falling on the $x = 0$, $y = 0$ coordinate). Step 3: Overlay all median centres to create a composite picture of all monthly fixes of all birds. Step 4: Calculate 95% MCP home-range for the month. NB: Each colour denotes location points of a different individual.

same models using only composite home-ranges of non-breeding birds. We did not compute monthly composite home-ranges of only breeding birds due to small sample sizes per month.

RESULTS

Spatial and temporal patterns of habitat use

Between April 2014 and June 2016, we captured and ringed 620 Red-capped Larks, which we re-sighted a total of 5515 times, with on average 8.8 ± 14.7 re-sightings per individual (range 1–105). Bird distribution varied with month, showing that larks spread throughout the study area at some times, whereas at other times they concentrated in particular parts of the study

area (Fig. 2), suggesting fission–fusion dynamics. The mean composite monthly home-range of Red-capped Larks was $58.0 \text{ ha} \pm 47.9$ (range 2.6–154.05, $n = 23$). The composite monthly home-range varied among months, with the smallest composite home-range in November 2015 being 75 times smaller than the largest in November 2014, based on 95% MCP. Composite home-range of breeding birds was 9.6 ha, whereas that of non-breeding birds was 142.9 ha (Fig. 3).

Individual bird home-range estimation and effect of sex on individual home-range

We estimated individual home-range sizes for 53 individuals based on a mean (\pm sd) 48.3 ± 18.1

(range = 31–115) fixes per bird. Mean individual home-range was $19.9 \text{ ha} \pm 17.1$ (range 1.7–79.6) for 95% kernel_{iscv}. Core areas of individual home-ranges at 50% kernel were $3.5 \text{ ha} \pm 3.7$ (range 0.3–18.5). None of these estimates was significantly influenced by the number of fixes per bird (95% kernel $F_{1,51} = 0.41$, $P = 0.52$; core areas $F_{1,51} = 1.16$, $P = 0.29$). They were also not affected by whether the location fixes were based on reading colour rings or tracking transmitters (95% kernel $F_{2,50} = 0.17$, $P = 0.85$; core areas $F_{2,50} = 0.00$, $P = 0.99$). Females had larger individual home-ranges and core areas than males (Fig. 4) but the differences were not significant (95% kernel $t_{37} = 0.36$, $P = 0.72$; core areas $t_{33} = 0.54$, $P = 0.59$).

Effects of weather, food availability and breeding on composite home-range

Evaluating how well weather, food availability and intensity of breeding explained variation in composite home-ranges of Red-capped Larks, we found that composite home-range significantly decreased with an increase in monthly nesting intensity (Fig. 5, Table 1). There was a near-significant decrease in composite home-range with an increase in EVI (Table 1). When we removed location fixes of birds with active nests, consistent with the analysis of breeding and non-breeding birds together, composite home-range decreased with an increase in monthly nesting index (Table 2). The other environmental factors were

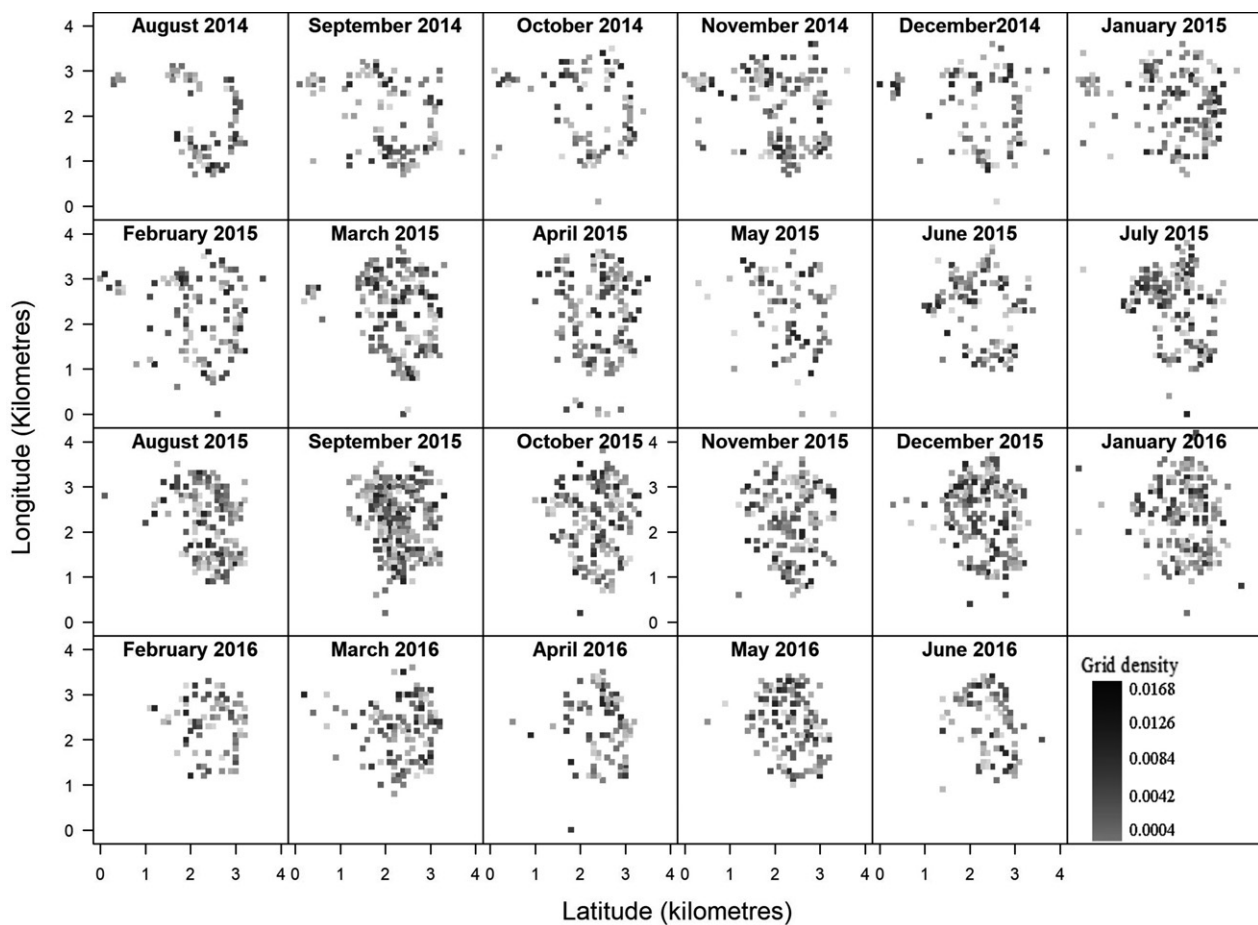


Figure 2. Spatial and temporal change in Red-capped Lark distribution per month within the study area during August 2014–June 2016. An individual bird is only represented once per grid per month, and variation in colour represents continuous transformation from low to high density as shown on the scale.

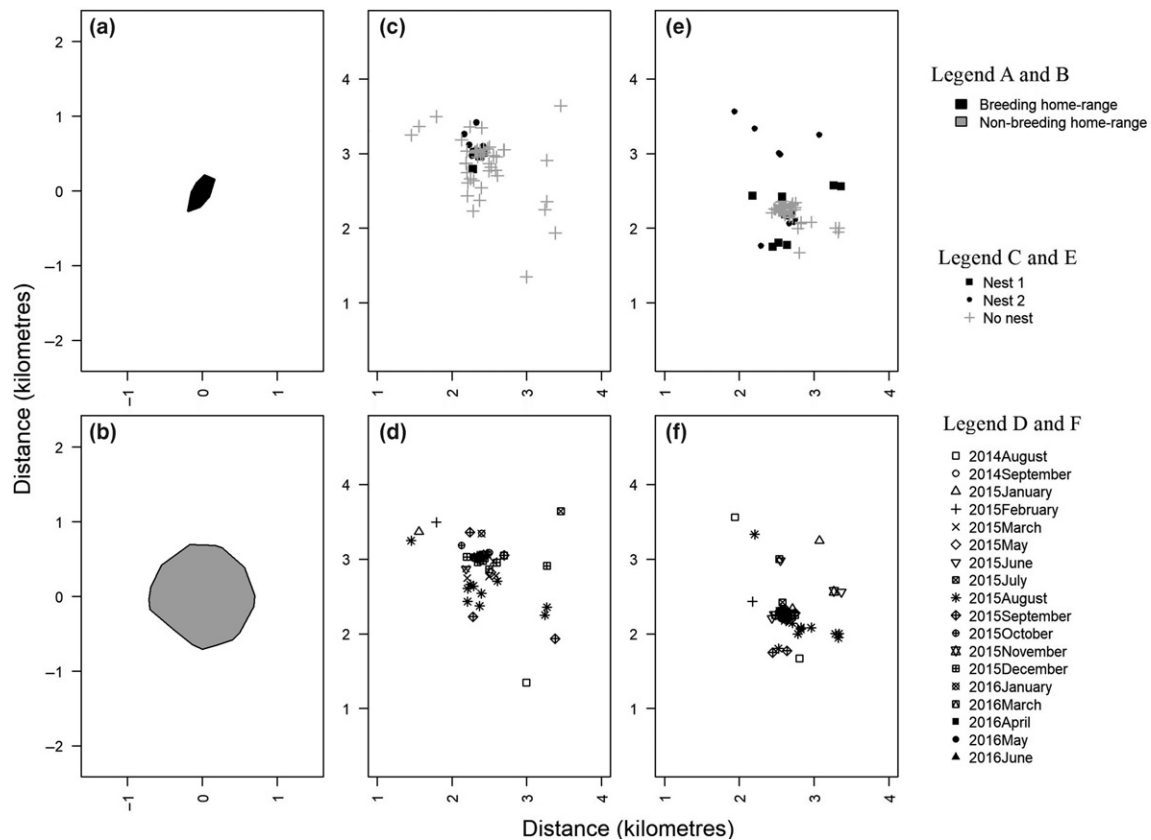


Figure 3. Composite home-range and location points of breeding and non-breeding Red-capped Larks in Kedong, showing size differences of 95% MCP composite home-range of breeding birds (black) compared with non-breeding birds (grey a and b); location fixes showing difference in locations of two Red-capped Larks when with active nests (c and e) and monthly location points of the same two birds during non-breeding periods, with each shape representing a different month (d and f). See specific legend for shape per plot categories.

not significantly related to composite home-ranges of Red-capped Larks.

DISCUSSION

In general, and in agreement with previous studies in this system (Ndithia *et al.* 2017a,b), we found no consistent pattern characteristic of seasonal environments in rainfall, temperature, vegetation, invertebrates or nesting throughout our two study years (see Appendix S5). Composite home-range sizes of resident equatorial Red-capped Larks showed substantial variation from month to month over the 23-month period of our study, partly associated with changes in environmental and social factors. Confirming the fission–fusion dynamics from breeding in pairs to flocking when not breeding, we found that the spacing behaviour and distribution of Red-capped Larks within our study area varied

among months. Individual home-ranges varied almost four-fold among individuals, but did not differ between sexes. Contrary to predictions, our combined analysis of non-breeding and breeding birds at the population level showed that composite home-range was not influenced by rainfall or invertebrate biomass, as potential indicators of food availability. However, conforming with our predictions, we found that composite home-ranges decreased in size with more vegetation, albeit weakly, and with higher breeding intensity. This suggested that Red-capped Larks had smaller home-ranges during breeding because movements are confined to the nest area. Surprisingly, restricting these analyses to non-breeding individuals only, we found the same associations with breeding intensity. To our knowledge, this is the first evidence that breeding intensity can affect the home-range sizes of non-breeding individuals. At the individual level,

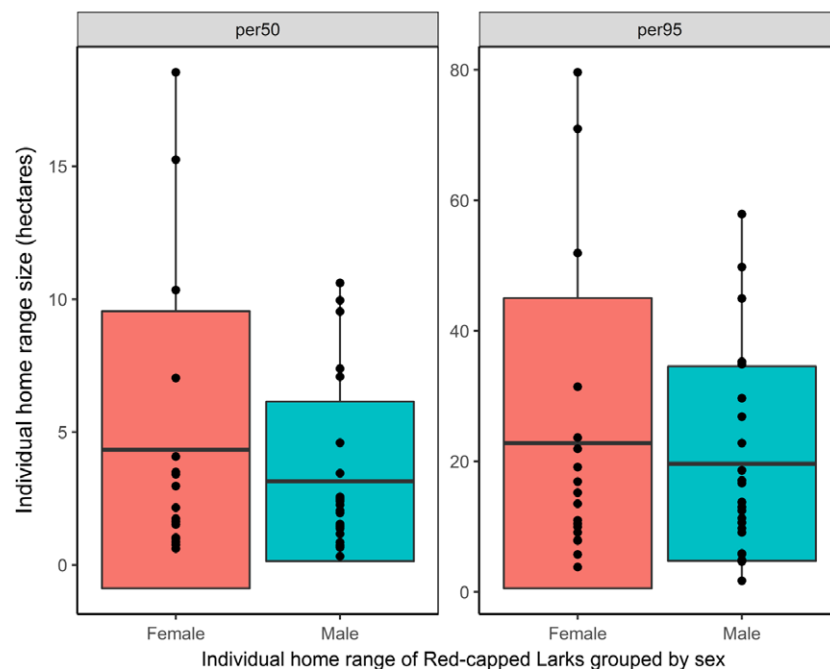


Figure 4. Average individual home-range and core area estimates for male and female Red-capped Larks. The central bold lines and coloured areas represent mean \pm sd, bars represent the range of values, and the black bold circles show the data points (individual Red-capped Lark home-ranges of the respective categories). [Colour figure can be viewed at wileyonlinelibrary.com]

home-ranges were 15-fold the size in non-breeding compared with breeding individuals.

Home-range and change in social organization from groups to pairs in Red-capped Larks

The mean individual home-range size of Red-capped Lark of 19.9 ha was larger than that reported for the phylogenetically related Dupont's Lark *Chersophilus duponti* (Garza *et al.* 2005), resident Afro-tropical insectivorous birds (Newmark *et al.* 2010) and similar-sized neotropical savannah species (Lopes & Marini 2006). The relatively large individual home-range may result from the fission–fusion behaviour in Red-capped Larks. Fusion into larger groups allows birds to exploit larger home-ranges, as shown in the Apostlebird *Struthidea cinerea* (Griesser *et al.* 2009). The observed temporal variation in movement and distribution within the habitat of Red-capped Larks could be attributed to fusion of breeding pairs into groups when not breeding, allowing birds to have access to a larger area and move longer distance for resources, e.g. for food, as shown in other birds (Griesser *et al.* 2009, Loretto *et al.* 2017). By assembling in flocks,

individual birds could enhance foraging efficiency, e.g. through a beater effect where feeding insects are flushed out by the other individuals within the group (Herremans & Herremans-Tonnoeyr 1997) or through finding optimal foraging patches within the habitat (Darrah & Smith 2014). Another advantage of flocking in Red-capped Larks may be to increase protection from predators via dilution of risk for individuals, predator confusion and increased vigilance shared by flock members (Darrah & Smith 2014, Ofstad *et al.* 2016).

Effect of weather, EVI, invertebrate biomass and breeding on composite home-range

The lack of influence of weather and invertebrate biomass on monthly variation in composite home-range from this study supports the conclusions by Ndithia *et al.* (2017a) that food availability and other resources may be sufficient year-round. Unlike temperate latitudes, our tropical system lacks the radical seasonal changes in weather and food availability experienced by birds (Skutch 1949). Because we did not observe a direct effect of invertebrates on composite home-range,

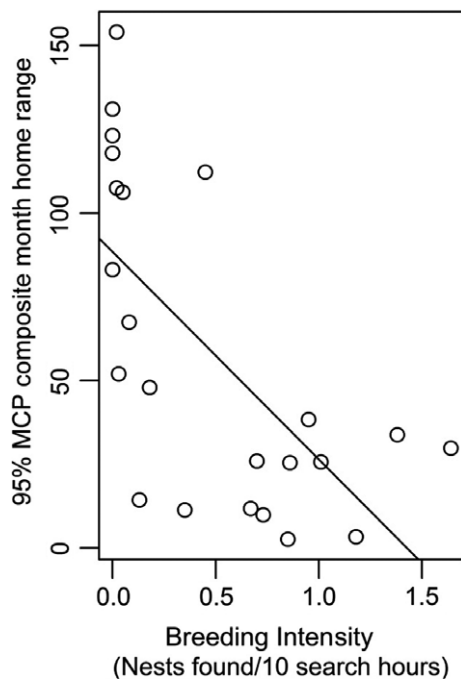


Figure 5. Variation in composite home-range size of Red-capped Larks with monthly breeding intensity.

decreased composite home-range with higher EVI, albeit weakly, may have reflected another mechanism than vegetation as a proxy for food availability. Instead, our results could be explained if vegetation indicates the physical characteristics of the habitat related to availability of nesting sites (Scott *et al.* 1998), and for protection from predators (Ofstad *et al.* 2016). With tropical conditions proposed to be characterized by high levels of predation (Skutch 1949), it is plausible that home-range may be highly influenced by habitat characteristics such as cover, moderating the risk of predation. During periods with less vegetation, Red-capped Larks may increase the size of the home-range to include areas with sufficient cover from predators.

Similar to our results, home-ranges in birds have been shown to vary with breeding status, some species reportedly showing an increase in home-range with breeding (Jahn *et al.* 2010, Kolts & McRae 2017), others a decrease (Willey & Van Riper Iii 2014, Morganti *et al.* 2017), and some show no variation between (Winiarski *et al.* 2017). The need to defend nest-sites, coupled with nest attendance and chick provisioning, may constrain movement of breeding Red-capped Larks to areas closer to their nests. The high cost associated with

Table 1. Model averaged estimates (\pm se) of the effects of breeding intensity (expressed as the total number of nests found in a month per 10 person-hours of effort), EVI, rainfall (mm), minimum (T_{\min}) and maximum (T_{\max}) temperature ($^{\circ}\text{C}$), and biomass of ground-dwelling and flying invertebrates on composite home-range of Red-capped Larks. Model-averaged estimates were derived using all models with weight ≤ 0.95 . A complete overview of model results with weight ≤ 0.95 is provided in Appendix S3.

	Estimate \pm se	95% confidence limits	P
Intercept	0.00 \pm 0.15	-0.33, 0.33	1.00
Breeding intensity	-0.59 \pm 0.19	-0.98, -0.20	< 0.01
Enhanced vegetation index	-0.42 \pm 0.22	-0.87, 0.03	0.07
Maximum daily temperature	0.14 \pm 0.20	-0.26, 0.55	0.48
Rain	-0.04 \pm 0.12	-0.28, 0.19	0.71
Ground invertebrate biomass	0.03 \pm 0.10	-0.18, 0.23	0.80
Minimum daily temperature	0.01 \pm 0.08	-0.17, 0.18	0.95
Flying invertebrate biomass	0.00 \pm 0.06	-0.13, 0.14	0.97

Table 2. Model-averaged estimates (\pm se) of the effects of breeding intensity (expressed as the total number of nests found in a month per 10 person-hours of effort), EVI, rainfall (mm), minimum (T_{\min}) and maximum (T_{\max}) temperature ($^{\circ}\text{C}$), and biomass of ground-dwelling and flying invertebrates, on composite home-range of non-breeding Red-capped Larks. Model-averaged estimates were derived using all models with weight ≤ 0.95 . A complete overview of model results with weight ≤ 0.95 is provided in Appendix S4.

	Estimate \pm se	95% Confidence limits	P
Intercept	-0.00 \pm 0.16	-0.34, 0.34	1.00
Breeding intensity	-0.56 \pm 0.21	-0.98, -0.13	0.01
Maximum daily temperature	0.18 \pm 0.23	-0.27, 0.64	0.43
Enhanced vegetation index	-0.39 \pm 0.24	-0.88, 0.09	0.11
Rain	-0.05 \pm 0.13	-0.32, 0.21	0.69
Ground invertebrate biomass	0.03 \pm 0.11	-0.19, 0.25	0.80
Minimum daily temperature	0.01 \pm 0.09	-0.19, 0.21	0.92
Flying invertebrate biomass	0.00 \pm 0.07	-0.14, 0.15	0.98

territorial defence may impose a maximum limit to the area that can be defended (Morganti *et al.* 2017).

To the best of our knowledge, we show for the first time that the home-range of Red-capped Larks that were not breeding was influenced by breeding intensity, indicating that home-range and associated movement behaviour of non-breeding individuals may also more strongly depend on breeding status of conspecifics than previously assumed. Nest area territoriality by breeding birds may exclude other birds from using areas near the nest; thus, the higher the number of breeding individuals, the bigger the size of defended areas (Nakamura 1995). This not only reduces the area available to non-breeding birds but also creates patchiness in areas accessible for them to forage, restricting them to smaller areas that are not defended by the breeding pairs.

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REFERENCES

- Anich, N.M., Benson, T.J. & Bednarz, J.C. 2010. Factors influencing home-range size of Swainson's Warblers in Eastern Arkansas. *Condor* **112**: 149–158.
- Baldwin, H.Q., Jeske, C.W., Powell, M.A., Chadwick, P.C. & Barrow, W.C. 2010. Home-range size and site tenacity of overwintering Le Conte's Sparrows in a fire managed prairie. *Wilson J. Ornithol.* **122**: 139–145.
- Barton, K. 2018. *MuMIn: Multi-Model Inference. R package Ver. 1.40.4*. Available at: <https://CRAN.R-project.org/package=MuMIn> (accessed 23 July 2018).
- van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M. & Myrsterud, A. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol.* **80**: 771–785.
- Bevanda, M., Fronhofer, E.A., Heurich, M., Müller, J. & Reineking, B. 2015. Landscape configuration is a major determinant of home range size variation. *Ecosphere* **6**: 1–12.
- Börger, L., Franconi, N., Ferretti, F., Meschi, F., Michele, G.D., Gantz, A. & Coulson, T. 2006. An Integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am. Nat.* **168**: 471–485.
- Burnham, K. & Anderson, D. 2002. *Model Selection and Multimodal Inference*. New York, NY: Springer.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**: 346–352.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**: 516–519.
- Darrah, A.J. & Smith, K.G. 2014. Ecological and behavioral correlates of individual flocking propensity of a tropical songbird. *Behav. Ecol.* **25**: 1064–1072.
- Fuller, A.K. & Harrison, D.J. 2010. Movement paths reveal scale-dependent habitat decisions by Canada lynx. *J. Mammal.* **91**: 1269–1279.
- Galipaud, M., Gillingham, M.A.F. & Dechaume-Moncharmont, F.-X. 2017. A farewell to the sum of Akaike weights: the benefits of alternative metrics for variable importance estimations in model selection. *Methods Ecol. Evol.* **8**: 1668–1678.
- Garza, V., Suárez, F., Herranz, J., Traba, E., García de la Morena, E.L., Morales, M.B., González, R. & Castañeda, M. 2005. Home range, territoriality and habitat selection by the Dupont's Lark *Chersophilus duponti* during the breeding and postbreeding periods. *Ardeola* **52**: 133–146.
- Germain, R.R., Schuster, R., Delmore, K.E. & Arcese, P. 2015. Habitat preference facilitates successful early breeding in an open-cup nesting songbird. *Funct. Ecol.* **29**: 1522–1532.
- Griesser, M., Barnaby, J., Schneider, N.A., Figenschau, N., Wright, J., Griffith, S.C., Kazem, A. & Russell, A.F. 2009. Influence of winter ranging behaviour on the social organization of a cooperatively breeding bird species, the Apostlebird. *Ethology* **115**: 888–896.
- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**: 699–711.
- Herremans, M. & Herremans-Tonnoeyr, D. 1997. Social foraging of the Forktailed Drongo *Dicrurus adsimilis*: beater effect or kleptoparasitism? *Bird Behav.* **12**: 41–45.
- Hijmans, R.J. 2016. Geographic data analysis and modeling. Available at: <https://CRAN.R-project.org/package=raster> (accessed 2 February 2018)
- Holland, A.E., Byrne, M.E., Bryan, A.L., DeVault, T.L., Rhodes, O.E. & Beasley, J.C. 2017. Fine-scale assessment of home ranges and activity patterns for resident Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*). *PLoS ONE* **12**: 1–16.
- Jahn, A., Pinto-Ledezma, J., María Mamani, A., DeGroot, L. & Levey, D. 2010. Seasonal home range size of Tropical Kingbird (*Tyrannus melancholicus*) in the southern Amazon Basin. *Ornitol. Neotrop.* **21**: 39–46.
- Kolts, J.R. & McRae, S.B. 2017. Seasonal home range dynamics and sex differences in habitat use in a threatened, coastal marsh bird. *Ecol. Evol.* **7**: 1101–1111.
- Lopes, L.E. & Marini, M.A. 2006. Home range and habitat use by *Suiriri affinis* and *Suiriri islerorum* (Aves: Tyrannidae)

- in the central Brazilian Cerrado. *Stud. Neotrop. Fauna Environ.* **41**: 87–92.
- Loretto, M.-C., Schuster, R., Itty, C., Marchand, P., Genero, F. & Bugnyar, T.** 2017. Fission-fusion dynamics over large distances in raven non-breeders. *Sci. Rep.* **7**: 380.
- Margalida, A., Pérez-García, J.M., Afonso, I. & Moreno-Opo, R.** 2016. Spatial and temporal movements in Pyrenean Bearded Vultures (*Gypaetus barbatus*): integrating movement ecology into conservation practice. *Sci. Rep.* **6**: srep 35746.
- Matsushita, B., Yang, W., Chen, J., Onda, Y. & Qiu, G.** 2007. Sensitivity of the enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) to topographic effects: a case study in high-density cypress forest. *Sensors* **7**: 2636–2651.
- Minderman, J., Reid, J.M., Hughes, M., Denny, M.J.H., Hogg, S., Evans, P.G.H. & Whittingham, M.J.** 2010. Novel environment exploration and home range size in Starlings *Sturnus vulgaris*. *Behav. Ecol.* **21**: 1321–1329.
- Morganti, M., Assandri, G., Aguirre, J.I., Ramirez, Á., Caffi, M. & Pulido, F.** 2017. How residents behave: home range flexibility and dominance over migrants in a Mediterranean passerine. *Anim. Behav.* **123**: 293–304.
- Mwangi, J., Ndithia, H.K., Kentie, R., Muchai, M. & Tieleman, B.I.** 2018. Nest survival in year-round breeding tropical Red-capped Larks (*Calandrella cinerea*) increases with higher nest abundance but decreases with higher invertebrate availability and rainfall. *J. Avian Biol.* **49**: e0164.
- Nakamura, M.** 1995. Territory and group living in the polygynandrous Alpine Accentor *Prunella collaris*. *Ibis* **137**: 477–483.
- Ndithia, H.K., Matson, K.D., Versteegh, M.A., Muchai, M. & Tieleman, B.I.** 2017a. Year-round breeding equatorial Larks from three climatically-distinct populations do not use rainfall, temperature or invertebrate biomass to time reproduction. *PLoS ONE* **12**: 1–18.
- Ndithia, H.K., Bakari, S.N., Matson, K.D., Muchai, M. & Tieleman, B.I.** 2017b. Geographical and temporal variation in environmental conditions affects nestling growth but not immune function in a year-round breeding equatorial lark. *Front. Zool.* **14**: 28.
- Newmark, W.D., Mkongewa, V.J. & Sobek, A.D.** 2010. Ranging behavior and habitat selection of terrestrial insectivorous birds in north-east Tanzania: implications for corridor design in the Eastern Arc Mountains. *Anim. Conserv.* **13**: 474–482.
- Nilsen, E.B., Pedersen, S. & Linnell, J.D.C.** 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecol. Res.* **23**: 635–639.
- Odum, E.P. & Kuenzler, E.J.** 1955. Measurement of territory and home range size in birds. *Auk* **72**: 128–137.
- Ofstad, E.G., Herfindal, I., Solberg, E.J. & Sæther, B.-E.** 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proc. R. Soc. B* **283**: 20161234.
- Orians, G.H. & Wittenberger, J.F.** 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* **137**: S29–S49.
- Pimentel, R. & Hansbauer, M.** 2013. A comparison of five techniques for attaching radio-transmitters to tropical passerine birds. *Rev. Bras. Ornitol. - Braz. J. Ornithol.* **16**: 6.
- R Core Team** 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Richardson, D.S., Jury, F.L., Blaakmeer, K., Komdeur, J. & Burke, T.** 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Mol. Ecol.* **10**: 2263–2273.
- Rolando, A.** 1998. Factors affecting movements and home ranges in the Jay (*Garrulus glandarius*). *J. Zool., Lond.* **246**: 249–257.
- Said, S., Gaillard, J.-M., Widmer, O., Débias, F., Bourgoïn, G., Delorme, D. & Roux, C.** 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos* **118**: 1299–1306.
- Scott, J.G., Lavallo, M.J., Storm, G.L. & Tzilkowski, W.M.** 1998. Summer habitat use by Ruffed Grouse with broods in Central Pennsylvania (Uso de Hábitat Veraniego en la Pennsylvania Central por Bonasa umbellus con Crías). *J. Field Orn.* **69**: 474–485.
- Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A.** 1999. Effects of sample size on kernel home range estimates. *J. Wildl. Manag.* **63**: 739–747.
- Silk, M.J., Croft, D.P., Tregenza, T. & Bearhop, S.** 2014. The importance of fission–fusion social group dynamics in birds. *Ibis* **156**: 701–715.
- Skutch, A.F.** 1949. Do tropical birds rear as many young as they can nourish? *Ibis* **91**: 430–455.
- Takano, L.L. & Haig, S.M.** 2004. Seasonal movement and home range of the Mariana Common Moorhen. *Condor* **106**: 652–663.
- Tieleman, B.I. & Williams, J.B.** 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol. Biochem. Zool.* **73**: 461–479.
- Tsao, D.C., Takekawa, J.Y., Woo, I., Yee, J.L. & Evens, J.G.** 2009. Home range, habitat selection, and movements of California Black Rails at tidal marshes at San Francisco Bay, California (Ámbito de Hogar, Selección de Hábitat y Movimientos de *Laterallus jamaicensis coturniculus* en Marismas en la Bahía de San Francisco, California). *Condor* **111**: 599–610.
- Van der Velde, M., Haddrath, O., Verkuil, Y.I., Baker, A.J. & Piersma, T.** 2017. New primers for molecular sex identification of waders. *Wader Study* **124**: 147–151.
- White, G.C. & Garrott, R.A.** 1990. *Analysis of Wildlife Radio-tracking Data*. London: Academic Press Ltd.
- Wickham, H.** 2009. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.
- Wiebe, K.L. & Gow, E.A.** 2013. Choice of foraging habitat by Northern Flickers reflects changes in availability of their ant prey linked to ambient temperature. *Ecoscience* **20**: 122–130.
- Willey, D.W. & Van Riper III, C.** 2014. Home range characteristics of Mexican Spotted Owls in the Rincon Mountains, Arizona. *Wilson J. Ornithol.* **126**: 53–59.
- Winiarski, J.M., Moorman, C.E. & Carpenter, J.P.** 2017. Bachman's Sparrows at the northern periphery of their range: home range size and microhabitat selection. *J. Field Ornithol.* **88**: 250–261.
- Worton, B.J.** 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**: 164–168.

- Worton, B.J.** 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manag.* **59**: 794–800.
- Zimmerman, D.A., Turner, D.A. & Pearson, D.J.** 2005. *Birds of Kenya and Northern Tanzania*. London: Christopher Helm.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S.** 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**: 3–14.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Appendix S1. Summary of tracked Red-capped Lark sightings showing number of location fixes per bird per month for the period August 2014–July 2016.

Appendix S2. Summary table of number of Red-capped Larks tracked per month, contributing points and their breeding status that were used to test for monthly home-range analysis.

Appendix S3. General linear models with effects of rainfall (rain), maximum temperature (T_{\max}), minimum temperature (T_{\min}), enhanced vegetation index (EVI), ground invertebrate biomass (GIB), flying invertebrate biomass (FIB) and breeding intensity (BI) on monthly home-range of Red-capped Larks.

Appendix S4. General linear models with effects of rainfall (rain), maximum temperature (T_{\max}), minimum temperature (T_{\min}), enhanced vegetation index (EVI), ground invertebrate biomass (GIB), flying invertebrate biomass (FIB) and breeding intensity (BI) on monthly home-range of non-breeding Red-capped Larks.

Appendix S5. Temporal variations during August 2014–June 2016.